Impact of flower and cone harvesting on seed banks and seed set of serotinous Agulhas Proteaceae

Penelope J. Mustart* and R.M. Cowling
Botany Department, University of Cape Town, Private Bag, Rondebosch, 7700 Republic of South Africa

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Inflorescences and cones of serotinous (canopy-stored seed) Proteaceae are extensively harvested by the wildflower industry from natural stands in fynbos of the Agulhas Plain, South Africa. This study investigated the impacts of harvesting on seed bank size and seed set of *Protea susannae* Phill., *P. obtusifolia* Beuk ex Meisn., *Leucadendron coniferum* (L.) Meisn. and *L. meridianum* I. Williams. Harvesting of inflorescences or cones by the stem-cutting method reduced the following season's infructescence (called 'cones') production in all species except *P. susannae*. Remaining current year cones of the harvested *Protea* spp. had greater insect predation levels, and unaltered or lower seed set, than those of unharvested plants. The seed set findings are not consistent with the hypothesis that seed numbers are nutrient-limited, since inflorescence harvesting represents a sink removal, and increased nutrients remaining in the plant would be available for increased seed set. Since repeated annual harvesting of 70% of current year inflorescences or fruit was estimated to result in severe seed bank depletion, it is suggested that lower levels of harvesting (not more than 50% of current inflorescences or cones) be performed in alternate years.

Die blomme en keëls van laatbloeiende Proteaceae (saad word in die kroon gestoor) word op 'n groot skaal deur die veldblomindustrie in die fynbos op die Agulhasvlakte, Suid-Afrika, ge-oes. Hierdie studie ondersoek die impak van oes op die grootte van die saadreserwes, en saadopbrengs per keël, van *Protea susannae* Phill., *P. obtusifolia* Beuk ex Meisn., *Leucadendron coniferum* (L.) Meisn. and *L. meridianum* I. Williams. Daar is gevind dat die oes van bloeiwyses of keëls deur die sny van die blomstele die volgende jaar se keëlproduksie verminder in al die spesies behalwe *P. susannae*. Die oorblywende keëls van die huidige jaar van ge-oeste *Protea* spp. het 'n toename in die roof van saad deur insekte, en dieselfde of 'n kleiner saadopbrengs per keël, as dié van onge-oeste plante, getoon. Die laasgenoemde vasstelling is nie in ooreenstemming met die hipotese dat saadgetalle voedselbeperk is, aangesien die verwydering van blomme voedseldreinering beperk, en die verhoogde voedingstowwe wat in die plant beskikbaar is, sou beskikbaar wees vir verhoogde saadopbrengs. Aangesien die herhaaldelike jaarlikse oes van 70% van die huidige jaar se blomme of vrugte 'n ernstige uitputting op die saadreserwes veroorsaak, word daar aanbeveel dat laer vlakke van oes (nie meer as 50% van die huidige jaar se blomme of keëls) al om die ander jaar uitgevoer word.

Keywords: Flower and cone harvesting, Proteaceae, seed bank impacts, seed set and within-plant nutrient availability.

*To whom correspondence should be addressed.

Introduction

Fynbos communities on the Agulhas Plain, South Africa, include many plant species which are economically valuable as cut flowers. Inflorescences and infructescences (cones) of many serotinous (canopy-stored seed) proteaceous species are picked in quantity by an expanding wildflower industry (Greyling & Davis 1989). Since seed is essential for post-fire population replacement of plants that are killed by fire, an understanding of harvesting impacts on seed banks and seed biology is needed to predict the effect of this harvesting on post-fire regeneration (van Wilgen & Lamb 1985; Cowling *et al.* 1986).

Cone or flower harvesting not only removes seeds or potential seeds, but also the nutrients they contain. Since both fynbos and south-western Australian Proteaceae grow on nutrient-poor soils, and yet produce seeds rich in nutrients (Pate *et al.* 1985), it has been suggested that seed numbers are limited by nutrient availability (Lamont *et al.* 1985; Cowling *et al.* 1986; Stock *et al.* 1989). Stock *et al.* (1989) found that inflorescence removal in *Banksia laricina* (Proteaceae) was associated with reduced inflorescence abortion and attributed this to increased within-plant nutrient availability. *Leucospermum parile* (Proteaceae) takes up nutrients in winter and stores them in tap roots and above-ground parts (Jongens-Roberts & Mitchell 1986). Phosphorus and nitrogen are later re-translocated from these reserves and concentrated in the seeds. Esler *et al.* (1989) also concluded that much phosphorus and nitrogen in seeds came from extra-floral nutrient stores. It can therefore be inferred that harvesting of Proteaceae inflorescences prior to seed maturation might lead to a relative increase in nutrients in the extra-floral plant reserves. If seed numbers are nutrient-limited, then the change in nutrient source–sink relations might allow remaining inflorescences to mature with increased seed numbers.

This study investigated the effect of harvesting on aspects of the seed ecology of proteaceous shrubs. Controlled harvesting was performed on previously unharvested populations of four serotinous species: *Protea susannae, P. obtusifolia, Leucadendron coniferum* and *L. meridianum*. All are

widely used in the wildflower industry. The effect of inflorescence or infructescence (here-after called 'cones') harvesting on vegetative regrowth, and on the following year's cone production, was investigated for all species. Harvesting effects on seed set and seed predation levels were investigated for the *Protea* spp. only. The hypothesis that harvesting of *Protea* spp. inflorescences (*i.e.* containing immature seed) would result in increased seed set in the remaining currently-matured infructescences, was tested. The relationship between total cone number and canopy volume was compared between harvested and unharvested populations of all species except *L. meridianum*. Harvesting impacts on seed bank size were determined, and guidelines for harvesting management are discussed.

Materials and methods

Study area and study species

The study site was situated on the coastal lowlands of the Agulhas Plain (34°35'S, 19°55'E), South Africa. Sampling was carried out in 18-year-old Proteoid Fynbos (Cowling *et al.* 1988) growing on soils derived from the Mio-Pliocene limestone of the Bredasdorp Formation (Thwaites & Cowling 1988). The climate of the area is mediterranean in type with 65% of the annual rainfall (mean, 452 mm) occurring between April and September.

The study species are seed-regenerating proteoid shrubs, 1.5 – 3.0 m tall. *Protea obtusifolia* and *Leucadendron meridianum* occur together on shallow, alkaline sands overlying limestone, and *P. susannae* and *L. coniferum* occur together on the adjacent, deep, moderately acid, colluvial sands derived from limestone. The *Protea* spp. are hermaphroditic, and inflorescences are picked between June and September, prior to seed maturation (Table 1). Female plants of the dioecious *Leucadendron* spp. are harvested in early autumn when inflorescences have matured into cones. Table 1 also shows the season of flowering, seed maturation times, and the proportion of the total seed bank occurring in cones of different ages.

Effect of experimental harvesting on cone production

Plant populations chosen for this study had never been previously harvested. Thirty plants of each species were randomly chosen, labelled and experimentally harvested in ways similar to those practised by the wildflower industry as follows:

(i) *Protea* species

During the 1987 flowering season the current year inflorescences were counted on all chosen individuals. Fifteen plants were left as controls (*i.e.* unharvested), and 15 were stem-harvested (cut 15 – 20 cm below the inflorescence) such that about 70% of the inflorescences were removed. The inflorescences produced in the flowering season after this experimental harvesting were counted (1988).

(ii) *Leucadendron* species

During March 1987 the current year cones were counted on all the chosen individuals. Each species was then divided into three groups of 10 plants each — one left as a control (unharvested), one for cone-harvesting (70% of current mature cones harvested immediately below the cones), and one for stem-harvesting (70% of current mature cones removed by cutting off the stem 15 – 20 cm below the cones). The number of cones produced in the season after harvesting was determined (1988).

Size-dependent reproduction in harvested and unharvested populations

In the above unharvested populations all the cones on 30 plants per species were counted. Plant height (= canopy depth) and canopy diameter were measured, and canopy volumes were calculated as the volume of an ellipsoid ($^4/_3\pi r_1 r_2^2$, where r_1 is the height/2 and r_2 is the diameter/2). In similar-aged vegetation in an adjacent area (1 – 2 km away) where plants had been commercially harvested over the past five years, measurements of total cones and canopy volume were obtained for *Protea susannae, P. obtusifolia* and *Leucadendron coniferum*. Harvested *L. meridianum* plants were unavailable since this species had not been commercially harvested for the past four years.

Effect of experimental harvesting on seed set and seed predation levels in *Protea* spp.

For each species five current cones per plant (15 experimentally harvested and 15 unharvested plants) were removed in April 1988. The number of apparently viable

Table 1 Harvesting season and selected reproductive attributes of four Agulhas Plain proteaceous shrubs

	Protea susannae	*Protea obtusifolia*	*Leucadendron coniferum*	*Leucadendron meridianum*
Harvesting season	June – Sept	July – Sept	March	March
Flowering season	April – August	July – September	late August	early August
Seed maturation time (months)[a]	5	4	3.5	3.5
Season when current seed is mature	Sept-Jan	Nov-Jan	mid-Dec	mid-Nov
Contribution to seed bank (%)[b]				
Current	22	51	40	38
One year old	34	28	35	25
> One year old	44	21	25	37

[a] Seed collected at intervals after flowering were considered mature when 90% of a test sample (75 seeds) germinated at 10°C dark: 10 h, 20°C light: 14 h (P.J. Mustart, unpublished data).

[b] Annual viable seed contribution as a percentage of total seed bank (Mustart 1991).

(embryo-filled and plump), aborted, and insect-damaged seeds were counted. The viable and damaged seed categories were each calculated as a percentage of the total (viable + aborted + damaged) seed number.

Harvesting impacts on seed banks

Harvesting impacts on seed banks were calculated using mean values obtained from unharvested plants of cone number per plant and viable seed per cone, and annual contributions of viable seed to the seed bank. Reduction in cone number due to harvesting, as well as the decrease in cone number in the season after harvesting, were incorporated in calculations of seed bank sizes in the year after harvesting. These were expressed as a percentage of the unharvested seed bank. The impact of two levels of harvesting were calculated: (i) removal of 70% of current cones only; and (ii) additional removal of 50% of one-year-old cones.

Statistical analyses

In order to determine the effect of harvesting on future inflorescence and cone production, annual individual plant variation was accounted for by using the difference (change) for each plant between inflorescence/cone numbers of the pre- and post-harvest season. Student's *t*-tests were performed on these changes to test for significances where necessary. Mann-Whitney tests were used to assess significance of differences between proportions of viable and damaged seed in harvested and unharvested plants.

Least-squares regression analysis was used to determine the relationship between canopy volume and cone number in the harvested and non-harvested populations. For all species, canopy volumes in the two populations overlapped extensively. Differences in the slopes and elevations of regression lines for different populations were determined using a *t*-test (Zar 1984).

Results

Effect of experimental harvesting on cone production

There was no vegetative regrowth below the cut stems of any of the four species. In both *Leucadendron coniferum* and *L. meridianum*, cone-harvesting did not result in decreased cone production the following year (similar means and large SEs) (Table 2). Stem-harvesting, however, resulted in a significant decrease in cone numbers. Harvested *Protea obtusifolia* plants also produced significantly fewer cones the season after picking, a finding not apparent in *P. susannae*.

Size-dependent reproduction in harvested and unharvested populations

Harvested shrubs had fewer cones than equivalent-sized unharvested shrubs (Figure 1). The slopes of the regression lines of harvested and unharvested plants were significantly different for *Leucadendron coniferum* ($P < 0.001$), but not for *Protea susannae* and *P. obtusifolia*. The elevations of regression lines for harvested and unharvested plants of the *Protea* spp. were significantly different ($P < 0.05$ and $P < 0.001$, respectively). The coefficients of determination, r^2, for harvested *P. susannae* and unharvested *P. obtusifolia* were both low (< 0.5).

Table 2 The effect of inflorescence harvesting of *Protea susannae* and *P. obtusifolia*, and cone harvesting of *Leucadendron coniferum* and *L. meridianum*, on cone production the following year[a]

	Cone numbers		
	1987 season	1988 season	Change[d]
Protea susannae			
Unharvested	54.7 (12.2)	36.8 (7.1)	–17.9 (32.6)
Stem-harvested[b]	65.1 (12.4)	32.5 (6.6)	–32.5 (35.8)NS
Protea obtusifolia			
Unharvested	8.1 (2.0)	4.7 (1.5)	–3.4 (4.8)
Stem-harvested[b]	14.5 (2.6)	1.3 (0.6)	–13.2 (10.0)*
Leucadendron coniferum			
Unharvested	198.9 (34.0)	245.8 (72.8)	46.9 (171.8)
Cone-harvested[c]	238.0 (78.8)	271.0 (75.1)	33.0 (65.2)
Stem-harvested[b]	223.1 (46.2)	120.8 (36.2)	–102.3 (145.8)*
Leucadendron meridianum			
Unharvested	70.7 (13.7)	116.9 (19.4)	46.2 (38.7)
Cone-harvested[c]	99.9 (28.4)	136.9 (37.3)	37.0 (54.2)
Stem-harvested[b]	68.6 (12.1)	56.8 (21.9)	–11.8 (49.7)*

[a] Cone numbers of the current year's crop were determined immediately before (March 1987) and the year after (March 1988) experimental harvesting. Cone numbers of unharvested controls were determined at the same time. Plant populations had never been harvested previously. Data are means (SE). n = 15 plants for *Protea* spp.; n = 10 for *Leucadendron* spp. Significance of differences in cone numbers between controls and stem-harvested plants in the year after harvesting was determined by *t*-tests on the change in cone number between 1987 and 1988.

[b] Stems cut 15 – 20 cm below inflorescences such that seventy percent of inflorescences removed.

[c] Seventy percent of current cones harvested.

[d] (1988 Cone numbers) – (1987 Cone numbers); NS, not significant; *, $P < 0.05$.

Effect of experimental harvesting on seed set and seed predation levels in *Protea* spp.

Whereas there was no difference in the percentage of viable seed per cone (seed set) between harvested and unharvested plants of *Protea obtusifolia*, harvested *P. susannae* had a significant, slightly lower fraction of seeds per cone than those of unharvested plants (Table 3). In both species there was an increase in the proportion of damaged seed in the cones of harvested individuals, although this change was not significant in *P. obtusifolia*. This increased predation in harvested plants (mean increase of damaged seed component was 10.3% for *P. obtusifolia* and 14.3% for *P. susannae*) represents a viable seed component of approximately 1.7 and 1.5% per cone, respectively, assuming viable seed of these species was eaten in proportion to mean fraction of viable seed present (Mustart & Cowling 1991a). Total viable seed of the harvested plants would then rise to 13.4 and 12.6%, respectively.

Harvesting impacts on seed banks

The most strongly serotinous species (*i.e.* those species which have the lowest contribution of current year's crop to the total seed bank) (Table 1) had seed banks which were least affected by 70% harvesting of current inflorescences and cones (Table 4). For example, *Protea susannae*, relying

on its current seed crop for only 22% of its total seed stores, had its seed bank reduced to 75%, whereas *P. obtusifolia*, with 50% in current cones, was reduced to 57%. Additional removal of half the one-year-old cones reduced seed banks of all species to about half, or less, of their original value.

Discussion

Effect of harvesting on cone production

These results showed that harvesting not only reduced the standing crop of canopy-stored seed, but also that the reduction could be carried over into the following season due to the lowered cone production following stem-harvesting. Since all species produce inflorescences terminally, and since no vegetative regrowth occurred from stems after stem-harvesting, it can be assumed that the post-harvest cone reduction was a consequence of the removal of vegetative modules containing future growth points. Rebelo and Holmes (1988) noted that commercially harvested *Brunia albiflora* (Bruniaceae), a serotinous fynbos shrub, bore fewer infructescences than unharvested plants of the same size. Our study also noted fewer cones on plants in commercially harvested populations of *Protea susannae, P. obtusifolia* and *Leucadendron coniferum* than on similar-sized unharvested plants (Figure 1). This is also likely to be due to the repeated annual removal of terminal growth points. Whereas harvested plants of the *Protea* spp. had consistently fewer cones than similar-sized, unharvested plants (similar slopes), the difference increased significantly with increasing canopy volume in *L. coniferum*. This could be related to high picking intensities of the larger, prolific cone-bearing plants of the latter species. It is also possible that older cones fall off the plant (harvesting of current cones would lead to a greater proportion of the total cone number comprising older cones). Whatever the cause, the vulnerability of this species to damage from stem-harvesting is heightened by this phenomenon. This relationship of plant size to reproductive output could be used as a guideline for recommended stem-harvesting intensities. Plants could be pruned to a prescribed minimum size which bears an adequate number of cones (*i.e.* containing sufficient seed for post-fire regeneration). Samson and Werk (1986) stress this approach of noting size-dependent effects on reproduction.

Table 3 Percentage viable seeds and insect-damaged seeds per current cone of control, unharvested and remaining current cones of experimentally harvested plants of *Protea susannae* and *P. obtusifolia*[a]

	Protea susannae	*Protea obtusifolia*
Percentage viable seeds per cone		
Unharvested	13.3 (2.1) (n = 15)	13.4 (3.1) (n = 13)
Harvested	11.1 (2.6)* (n = 14)	11.7 (2.6)NS (n = 14)
Percentage damaged seeds per cone		
Unharvested	13.5 (2.2) (n = 15)	23.3 (3.5) (n = 13)
Harvested	27.8 (3.5)* (n = 14)	33.6 (5.0)NS (n = 14)

[a] Plants were harvested such that 70% of current inflorescences were removed during their respective flowering seasons. Mature cones of the following season were analysed for viable, non-viable and damaged seed components. Data are means (SE). Significance of differences between unharvested and harvested values was determined by Mann-Whitney tests. n, number of plants; NS, not significant; *, $P < 0.05$.

Table 4 Calculated scenarios showing the proportion of unharvested seed bank remaining in the year after two different levels of harvesting[a]

Harvesting levels	*Protea susannae*	*Protea obtusifolia*	*Leucadendron coniferum*	*Leucadendron meridianum*
70% current cones removed	75	57	65	62
70% current & 50% one-year-old cones removed	61	44	53	54

[a] Post-harvest seed bank sizes are expressed as a percentage of unharvested seed bank sizes, and are mean values. n = 30.

Does nutrient sink removal increase seed set?

If the viable seed number is determined by within-plant available nutrients, it would be expected that seed set per cone in remaining current year cones of harvested *Protea* spp. would be higher than those of unharvested control plants. Experimentally harvested plants had seed set per cone either similar to (*P. obtusifolia*), or lower than (*P.*

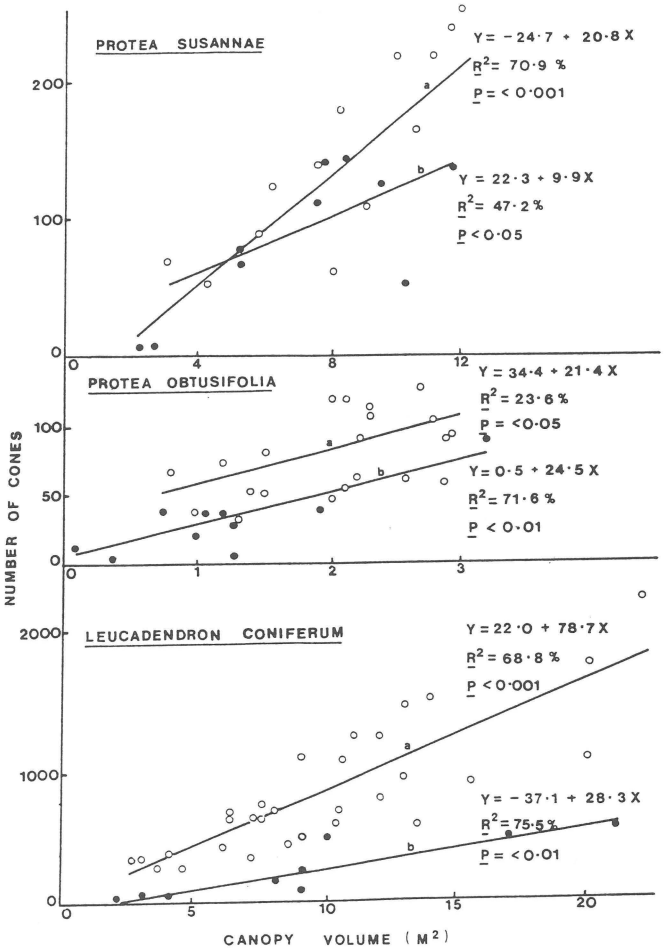

Figure 1 Relationships between total cone numbers per plant, and canopy volumes (m^3) in unharvested and commercially harvested populations of *Protea susannae, P. obtusifolia* and *Leucadendron coniferum*. Harvested plants had been stem-harvested over the past 5 years. Regression lines: a, unharvested plants; b, harvested plants; ○, unharvested plants; ●, harvested plants.

susannae) those of unharvested plants (in both cases effectively resulting in *lower* current seed numbers per harvested plant, since cone numbers were less). The estimated viable seed component of the increased seed predation found in harvested plants would not change this trend. This finding that despite a nutrient sink removal, there was no increase in the number of viable seeds forming in the fewer remaining cones, is not consistent with the hypothesis that seed numbers are determined by nutrient levels. These conclusions differ from those of Stock *et al.* (1989) who observed that experimental removal of inflorescences in *Banksia laricina* led to decreased abortion levels of the remaining blooms, resulting in unaltered seed numbers *per plant*, compared to unharvested controls. Infloresence abortion in our two *Protea* spp. was minimal, so mechanisms for altering seed numbers per plant (if, in fact, they do exist) would be different, with possible change being effected at the level of number of seeds per cone rather than in numbers of infructescences per plant. Ayre and Whelan (1989) have suggested that there are independent mechanisms for controlling fruit set operating *via* excess flowers per inflorescence, and *via* excess inflorescences per plant. There are many alternate explanations for the low seed set in Proteaceae, other than nutrient limitation. These include pollen or pollinator limitation, lack of space, high insect predation levels, or post-zygotic abortion to produce high-quality seeds in an outcrossing system (Bierzychudek 1981; Collins & Rebelo 1987; Zimmerman & Pyke 1988; Wallace & O' Dowd 1989; Ayre & Whelan 1989). Low seed set in *Protea* spp. has also been proposed as a predator evasion strategy (Coetzee & Giliomee 1987; Mustart & Cowling 1991a).

Effect of harvesting on seed predation

Protea obtusifolia seed predation levels were higher in the remaining current year cones of experimentally harvested plants than in those of unharvested controls. The same trend (though not significant) was found for *P. susannae*. It is possible that insect predators of low mobility emerging from older cones on the same plants would concentrate on the lower numbers of cones. This finding is in contrast to the decreased predation that has been reported to occur with successive, annual commercial harvesting of populations of *Protea repens* over five years, when the number of damaged blooms decreased from 80% to 15% (A. Gray, pers. commun.). This finding can be attributed to the removal of sources of insect infestation in that there are fewer old cones. A decrease in predation has also been reported in harvested *P. magnifica* (= *barbigera*) plants (Myburgh *et al.* 1974).

Harvesting impacts on seed banks

In serotinous species, such as those in this study, the proportion of the seed bank removed by flower or current cone harvesting depends on the size of older stored seed reserves (*i.e.* the degree of serotiny). It has been shown that these canopy-stored seed reserves retain viability for at least four to five years in cones (Mustart & Cowling 1991b). The size of these reserves depends in turn on the intensity and frequency of harvesting in earlier years. In this study, seed loss was calculated using two harvesting levels imposed on previously unharvested plants of known patterns of seed storage. Since harvesting by the wildflower industry is repeated in successive years, thus altering these patterns of seed storage, it is more difficult to make generalizations about the extent of seed bank depletion. However, this study has shown that seed bank reductions can be severe in weakly serotinous species. Repeated annual harvesting could thus result in serious seed bank depletion. *Protea susannae* could be more resilient to harvesting since it relies on current seed production to a lesser extent (22% of seed bank) than the other species (38 – 51%) (Table 1). In addition, this species is not in high demand, unlike the co-occurring *Leucadendron coniferum*. The latter species retains only 25% of its seed bank in cones older than 2 years, and the possibility of a severe reduction in seed bank size by harvesting exists. According to lottery model theories, selection operating on seeds for occupation of empty post-fire space is random, and co-existence is mediated by reproductive similarity, such as similar seed numbers (Fagerstrom 1988). In harvested populations, such a post-fire lottery would favour *P. susannae*. Similarly, sustained harvesting of *P. obtusifolia* would reduce its ability to compete for establishment sites with the unharvested *L. meridianum*. The increasing numerical advantage of *P. susannae* and *L. meridianum* seedlings over several post-fire regeneration events would lead to the eventual elimination of *L. coniferum* and *P. obtusifolia*, respectively, in harvested areas. There is evidence of a decline in post-fire recruitment of *L. coniferum* in mixed stands with *P. susannae* (R. Yeaton & R.M. Cowling, unpublished data).

It is not known how many seeds are required for adequate post-fire regeneration. The variability in Proteaceae post-fire seedling : pre-fire parent ratios is largely unexplained (Midgley 1989), though much has been attributed to season of burn (Bond *et al.* 1984; van Wilgen & Viviers 1985). The species in this study can have several thousand canopy-stored seeds per plant, yet only one successful seedling is needed for replacement. It is possible that seed not lost through harvesting would be lost in density-dependent seedling interactions. At the other extreme, poor establishment under adverse conditions could lead to local extinction. We suggest a cautious approach, and that seed bank sizes should not be decreased by more than 50%. This approximates the degree (22 – 51%, for these species) by which unharvested seed banks would be reduced in the event of an unseasonable fire in late spring/early summer, before the current seed has matured (Table 1). We suggest that harvesting levels do not exceed more than fifty percent of current inflorescences or cones. In the light of the subsequent lowered cone production in the post-harvest year, we further suggest that stem-harvesting be performed in alternate years. This would allow some measure of vegetative and subsequent reproductive restoration.

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